

Species response curves along environmental gradients. A case study from SE Norwegian swamp forests

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Abstract. Vegetation science has relied on untested paradigms relating to the shape of species response curves along environmental gradients. To advance in this field, we used the HOF approach to model response curves for 112 plant species along six environmental gradients and three ecoclines (as represented by DCA ordination axes) in SE Norwegian swamp forests. Response curve properties were summarized in three binary response variables: (1) model unimodal or monotonous (determinate) vs. indeterminate; (2) for determinate models, unimodal vs. monotonous and (3) for unimodal models, skewed vs. symmetric. We used logistic regression to test the influence, singly and jointly, of seven predictor variables on each of three response variables. Predictor variables included gradient type (environmental or ecocline) and length (compositional turnover); species category (vascular plant, moss, *Sphagnum* or hepatic), species frequency and richness, tolerance (the fraction of the gradient along which the species occurs) and position of species along each gradient. The probability for fitting a determinate model increased as the main occurrence of species approached gradient extremes and with increasing species tolerance and frequency and gradient length. Appearance of unimodal models was favoured by low species tolerance and disfavoured by closeness of species to gradient extremes. Appearance of skewed models was weakly related to predictors but was slightly favoured by species optima near gradient extremes. Contrary to the results of previous studies, species category, gradient type and variation in species richness along gradients did not contribute independently to model prediction. The overall best predictors of response curve shape were position along the gradient (relative to extremes) and tolerance; the latter also expressing gradient length in units of compositional turnover. This helps predicting species responses to gradients from gradient specific species properties. The low proportion of skewed response curves and the large variation of species response curves along all gradients indicate that skewed response curves is a smaller problem for the performance of ordination methods than often claimed. We find no evidence that DCA ordination increases the unimodality, or symmetry, of species response curves more than expected from the higher compositional turnover along ordination axes. Thus ordination axes may be appropriate proxies for ecoclines, applicable for use in species response modelling.

Keywords: Boreal forest; DCA; Ecocline; Environmental factor; Gradient property; Logistic regression; Modelling; Peatland.

Abbreviations: GAM = Generalized Additive Model; GLM = Generalized linear model; HOF = Huisman-Olff-Fresco; LNMDS = Local Non-metric Multidimensional Scaling.

Nomenclature: Lid & Lid (1994); Frisvoll et al. (1995); Krog et al. (1994), except for *Polytrichastrum* G.L.Sm., which is not recognized as distinct from *Polytrichum* Hedw. Several groups of related taxa were treated collectively.

Introduction

Properties of species response curves along gradients have been much debated for 25 years. Several propositions for relationships between gradient and species properties and species response curve shapes have been forwarded. For instance, Austin et al. (1990, 1994) found more skewed response curves for species with optima near gradient end points and Minchin (1989) found differences in response curve shape among species (structural) groups. Austin (1987) warned that response curve characteristics might be confounded by variation in species richness along gradients. A general understanding of the relative importance of factors governing the distribution of species response curve shapes along environmental gradients has not been reached (Austin 1976, 1987; Austin & Gaywood 1994; Lawesson & Oksanen 2002) except for the fact that species differ with respect to type and shape of response curves (Austin 1976, 1990; Minchin 1989; Huisman et al. 1993; Bongers et al. 1999; R. Økland et al. 1999) and that the relative frequency of monotonous and unimodal response curves shifts in favour of the latter when the amount of compositional turnover along gradients increases (R. Økland 1990). Austin (1999a, b) thus con-

cluded that a theoretical basis for vegetation science, built on general rules for species responses to gradients, is still not available and that much ecological research is based on still untested paradigms. Developments in theoretical vegetation science have been hampered by a lack of empirical data of sufficient relevance and quality and lack of appropriate statistical methods for evaluating species response curve shapes with respect to environmental gradients (Austin 1980; Austin & Smith 1989; van der Maarel 1989; Austin et al. 1994; Oksanen & Minchin 2002). Among the many techniques that can be used to model species response curves, the Huisman-Olff-Fresco (HOF) models (Huisman et al. 1993) have been shown in two recent papers (Lawesson & Oksanen 2002; Oksanen & Minchin 2002) to perform better than other methods such as Generalized Linear Models (GLM), Generalized Additive Models (GAM) and β functions. Applying HOF modelling to empirical data of high quality from different ecosystems thus makes developments in theoretical vegetation science possible (Lawesson & Oksanen 2002; Oksanen & Minchin 2002).

Species do not respond to single environmental factors but to complex gradients consisting of varying environmental factors (Whittaker 1956; R. Økland 1990, 1992). No unambiguous method exists for quantification of complex gradients. These have, most often, been approximated by ecologically interpreted Detrended Correspondence Analysis (DCA) axes scaled in robust units of compositional turnover (Peet et al. 1988; R. Økland 1986a, 1990, 1992). Species response curves with respect to ordination axes differ from curves with respect to measured environmental variables correlated with these axes in being more symmetric (R. Økland 1986b; Minchin 1989) and more predictable (Ejrnæs 2000). It is not yet known if these differences are brought about by the ordination method(s) as such or if they reflect differences between complex and single environmental gradients.

Ordination techniques are important tools for summarizing species composition patterns and generating hypotheses in ecology. Ordination axes are correlated with measured environmental variables to study vegetation-environment relationships (ter Braak & Prentice 1988; R. Økland 1990, 1996). Interpreted ordination axes are used as substitutes for complex gradients with respect to which single species distributions are described (Oksanen 1987; Carleton 1990; Brunet et al. 1996; T. Økland 1996; Rydgren 1996; R. Økland et al. 2001). Metric ordination methods are based on the assumption that all species have the same response to the axes (which are latent variables or hypothetical environmental gradients); linear in principal component analysis (PCA) and unimodal in correspondence analysis (CA) and DCA (ter Braak & Prentice 1988). Among-species variation in response curve shape inevitably occurs (Austin 1986; R. Økland 1990), making

this assumption an over simplification. Deviation of actual species responses from the general species response model implicit in the ordination method thus imposes a risk of unknown magnitude that the true gradient structure is distorted during the ordination process (Minchin 1987; Wartenberg et al. 1987). This 'lack-of-fit-of-data-to-model variation' is often expressed on ordination axes without ecological meaning; polynomial distortion axes (Gauch 1982; R. Økland 1999). Ordination techniques based on a unimodal response model have attained high popularity because the risk of producing distorted ordinations is generally lower than with linear methods (Kent & Ballard 1988). However, criticism has been raised against treating all species as having symmetric unimodal response curves with respect to all environmental gradients (Austin 1976, 1980, 1999b; Minchin 1989). Thus, there is a need for more knowledge of the distribution of response curve shapes, to enhance predictability of ordination method performance, for the relative merits of ordination techniques to be properly evaluated and, in general, for plant community theory to be improved (Austin & Smith 1989; Austin et al. 1994; Austin & Nicholls 1997; Austin 1999b; Oksanen & Minchin 2002).

Swamp forests are biodiversity oases in the boreal forest landscape (Ohlson et al. 1997; Hörnberg et al. 1998), with a larger species pool and higher species densities than the surrounding matrix of forests on mineral soil (R. Økland et al. 2001). This is particularly the case for nutrient-rich swamp forests which, during their development, have typically accumulated unique sets of species (R. Økland et al. 2003). With their considerable variation in ecological conditions on different scales and large species pools, boreal swamp forests provide data well suited for exploring species response curves along environmental gradients.

Our study is based on a monographic study of vegetation-environment relationships in 150 1-m² plots distributed on 11 SE Norwegian swamp forests dominated by *Picea abies* (R. Økland et al. 2001); all plots were analysed with regard to the full autotrophic species composition and environmental data recorded. Two main and one minor gradient in species composition were found by ordination. In the present study we use the HOF modelling approach (Huisman et al. 1993; Oksanen & Minchin 2002) to fit response curves to 112 boreal swamp-forests species, with respect to important single environmental gradients as well as complex gradients as approximated by DCA ordination axes. Our main aim is to test the extent to which properties of species response curves can be predicted from gradient and species characteristics. In doing so, we aim to improve the theoretical basis for ordination methodology and contribute to theoretical vegetation science by re-evaluating the potential for generalizing about species response curve shapes.

Material and Methods

Study area

The study was carried out in Østmarka Nature Reserve (ca. 12.5 km²), Akershus county, SE Norway (for details see T. Økland 1990, 1996; Rydgren 1997; R. Økland et al. 2001). The bedrock is Precambrian, and quartz diorite, tonalite and gneisses of diverse origins dominate (Sigmond et al. 1984). The bedrock is mostly covered by thin quaternary deposits of glaciofluvial origin (Holmsen 1951; Sigmond et al. 1984). The area is covered by coniferous forest, which occur interspersed with topogeneous mires, swamp forests and small lakes. Due to large topographic variation over short distances, the variation in forest types on mineral soil is extensive. The area has been selectively cut, most recently ca. 60 yr before the data were collected (B. Økland 1994).

The climate is slightly suboceanic with annual mean precipitation of ca. 800 mm and annual mean temperature of 3.9 °C (1961–1990, cf. Aune 1993; Førlund 1993).

Recording of species

We distributed the sample plots by a restricted random procedure, over 11 swamp forests in Østmarka Nature Reserve (see R. Økland et al. 2001). In each sample plot, presence/absence of soil and peat dwelling vascular plants (the field layer; including lignified species < 80 cm high), bryophytes and lichens (the bottom layer) was recorded in each of 16 subplots (0.0625 m²). Frequency in these subplots was used as a measure of species abundance (T. Økland 1988; R. Økland 1990). We used data for 112 (from a total of 212) species occurring in eight (5% of total) or more sample plots to analyse species response curves. Of these, 49, 36, 9 and 18, respectively, were vascular plants, mosses (excluding *Sphagnum*), *Sphagnum* and hepatics.

Recording of environmental gradients

Of 53 explanatory variables in five groups (topographic, tree influence, water table, water chemical and physical properties measured *in situ* and soil chemical and physical variables) that were measured or calculated for each sample plot (see R. Økland et al. (2001) for full details), six (at least one from each group) were chosen as *environmental gradients* to which observations of species abundance were related. These six, all related to species performance as demonstrated by high correlations with DCA ordination axes (see below), were:

1. *Slope*, maximum slope in 25 cm, measured as degrees [400-degree

circle; corresponds to SlopeMa25 in R. Økland et al. (2001)].

2. The tree influence index (values increasing from low to high tree influence) based on all trees, including living and standing, fallen dead and stumps: *TreeInf*; corresponds to TreeInfAll in R. Økland et al. (2001), obtained by use of the model developed by R. Økland et al. (1999).

3. Median depth to the water table: *WatTab*; corresponding to WatTab50 in R. Økland et al. (2001), recorded as the depth from the surface of the bottom layer to the level exceeded by water for half the 1998 growing season. Water table measurements were made at ten day intervals throughout the ice free season of 1998 in a tube inserted into the peat.

4. Water pH, measured *in situ* in groundwater wells on 27 May 1998: *pHWat*; corresponding to WatpH0527 in R. Økland et al. (2001) by a DigiSense S938-50 instrument with a Cole-Palmer G25 probe (Cole-Palmer Instrument Co., Vernon Hills, IL, USA).

5. Soil pH, measured in the laboratory in an aqueous suspension of a sample from the upper 5 cm of the humus layer that was dried, ground and sifted with 2 mm mesh: *pHSoil*; corresponding to Soil-pH-H₂O in R. Økland et al. (2001).

6. *Total N*: N; corresponding to HumusN in R. Økland et al. (2001), measured as total weight % of nitrogen, divided by loss on ignition of the humus sample.

Recording of ecoclines as represented by DCA axes

The data set – 212 species and 150 plots – was subjected to parallel DCA (Hill 1979) with program CANOCO, Vers. 4.0 (ter Braak & Šmilauer 1998) and four-dimensional LNMDS (Local Non-metric Multidimensional Scaling; Minchin 1987) with program DECODA, Vers. 2.04 (Minchin 1990) (see R. Økland et al. (2001)).

Comparison of DCA and LNMDS ordination results revealed three pairs of strongly correlated axes (DCA 1 and LNMDS 1; DCA 2 and LNMDS 2; DCA 4 and LNMDS 3) that were also interpretable in environmental terms. DCA 3 mainly separated plots from different swamp forest localities without being related to differences in measured environmental variables (R. Økland et al. 2003), the fourth LNMDS axis was not interpretable. The three environmentally interpretable gradients were:

1. Gradient related to soil acidity and nutrient concentrations (Kendall's τ of DCA 1 with N = 0.484; with pH-Soil = 0.423; with pH-Wat = 0.365; all $P < 0.0001$);

2. Gradient related to depth to the ground water table and the meso-scale topographic relief of the swamp forest surface (Kendall's τ of DCA 2 with WatTab = 0.536; with TreeInf = 0.351; both $P < 0.0001$); 3. Gradient related to surface microtopography, extending from flat, lawn like areas dominated by large bryophytes to more strongly sloping sites dominated by small mosses and hepatics (τ of DCA 4 with Slope = 0.264, $P < 0.0001$).

The correspondence between results obtained by the two fundamentally different ordination methods was taken as a strong indication that the three (pairs of) axes represented the main compositional gradients in the data set (R. Økland 1990, 1996; R. Økland et al. 2001). Because these axes were well interpretable in environmental terms, we consider them as good substitutes for main ecoclines (gradients in species composition and complex environmental gradients, considered jointly; Whittaker 1967).

Fitting species response curves by HOF modelling

Species response curves were fitted to the data abundances for 112 species and nine gradients (1008 species-gradient combinations) with the HOF program vers. 2.3 (J. Oksanen pers. comm.; <http://cc.oulu.fi/~jarioksa/>). This program fits HOF models (Huisman et al. 1993) to species abundance data, using maximum likelihood estimation with Poisson error. The models tested by the HOF program were, in order of decreasing complexity:

1. Model V: a skewed unimodal response curve;
2. Model IV: a symmetric unimodal response curve;
3. Model III: a monotonous response with a plateau;
4. Model II: a monotonous response curve;
5. Model I: indeterminate (no trend).

The program starts with the most complex model V, then proceeds by fitting successively simpler models until a simplification of the model implies a reduction in the variation explained (change of deviance) significant at $P < 0.05$. The final selection of model introduces a slight bias against model III (Oksanen & Minchin 2002).

Statistical analyses

Analyses were made using S-PLUS version 6.0 for Windows (Anon. 2001). For statistical modelling, we used GLM (McCullagh & Nelder 1989; Myers et al. 2002; Venables & Ripley 2002), a family of regression techniques by which a set of predictor variables (in our study, typically species and/or gradient properties) can be tested for their ability to account for variation in a response variable, such as a species response curve type (Venables & Ripley 2002). In all nested GLM models, parameters $\hat{\beta}_i$ were tested (null hypothesis: $\beta_i = 0$, against the two-tailed alternative) by the F -statistic

$$F = \frac{(D_{i-1} - D_i) df_i}{D_i (df_i - df_{i-1})} \quad (1)$$

where D_{i-1} and D_i are the deviances of models M_{i-1} and M_i (deviance is -2 times the summed log-likelihood of a model) and df_i and df_{i-1} are the degrees of freedom remaining after fitting models i and $i-1$. The F -test was chosen because it compensates for under or overdispersion (scale parameter $\theta_i \neq 1$ in models; Myers et al. 2002).

Detection of variation in species density (species richness at the plot scale; Grace 1999) along gradients as a factor influencing species response curve properties (Austin 1987) was allowed for by modelling the variation in species density along each of the nine gradients; the expected value of species density (response variable) was related to gradient position of the 150 plots (predictor variable). Because the response variable was species counts, logarithmic link function and Poisson distribution of errors were used (Venables & Ripley 2002). A non-linear rela-

tionship between predictor and response was allowed for by testing up to second-order functions of the predictor. Information on the range of variation in expected species richness encountered along each gradient was obtained as fitted values from a locally weighted regression scatterplot smoother (LOESS; Venables & Ripley 2002), as provided by the scatter smooth function in S-PLUS (see Venables & Ripley 2002).

The influences of gradient and species properties on species response curve shapes were analysed by separate logistic regression modelling (GLM with logit link function and binomial distribution of errors; Venables & Ripley 2002) of three binary response variables, constructed to describe the shape of the response curves fitted by HOF (112 species \times 9 gradients): (1) the model (**mod**) variable; **mod** = 1 if a monotonous or unimodal model (HOF models II, III, IV or V) was fitted, **mod** = 0 if the response model was indeterminate (HOF model I); (2) the unimodality (**umod**) variable which was recorded for all 820 response curves with **mod** = 1; **umod** = 1 if a unimodal model (HOF models IV or V) was fitted, **umod** = 0 if the fitted model was monotonous and (3) the skew (**sumod**) variable which was recorded for all 450 response curves with **umod** = 1; **sumod** = 1 if a skewed unimodal model (HOF model V) was fitted, **sumod** = 0 if the fitted model was symmetric unimodal. Logistic regression of the binary response variables models the probability for response variable = 1 as a function of predictor variables.

Seven predictor variables were used in the modelling, two of which (1 and 2) described the gradients, three (3, 4, 5) described the species and two (6 and 7) described gradient specific species properties:

1. Gradient type (**grtyp**), a factor with two levels (**grtyp** = 1 for ecoclines (DCA axes), **grtyp** = 2 for environmental gradients).
2. Gradient length (**grlen**), in S.D. units of compositional turnover; for environmental gradients obtained by linearly rescaling the gradients (cf. R. Økland 1990), one in turn, by subjecting the full species composition to DCCA (Detrended Canonical Correspondence Analysis; ter Braak 1986) with one constraining variable, using CANOCO; for ecoclines obtained as the length of the DCA axis in S.D. units. The length of non-linearly rescaled DCA and DCCA axes is a robust measure of the compositional turnover (R. Økland 1986a, 1990), one aspect of α diversity (Vellend 2001).
3. Species category (**spcat**), a factor with four levels (**spcat** = 1 for vascular plants, **spcat** = 2 for mosses except *Sphagnum*, **spcat** = 3 for *Sphagnum*, **spcat** = 4 for hepatics).
4. Species frequency (**spfr**), the frequency of the species in the 150 plots, recorded on a 0–1 scale.
5. Species richness (**sprich**), the species density (number of species per unit area) of sites in which the focal species occurs, estimated as the weighted average of species density in plots containing the focal species, using the focal species' subplot frequencies as weights.
6. Species tolerance (**sptol**), the fraction of a given gradient along which a given species occurred. Note that given as relative values (on a 0–1 scale), **sptol** will be inversely related to gradient length and that this relationship will be strongest and most regular for gradients that are longer than the mean tolerance of species (ca. 4 S.D. units; R. Økland 1990).

7. Species optimum (**sptol**), the relative point of gravity of each species along each gradient. The **sptol** variable was calculated from weighted averages of plot positions along the gradient, using the focal species' subplot frequencies as weights.

Because weighted averaging regression forces estimated optima of all species within the sampled portion of a gradient (ter Braak & Looman 1986), only the relative positions of species may be realistically estimated this way. For each gradient, we ranked the 112 species by weighted average position, and transformed the ranks to an index of the relative position of a species' optimum relative to gradient mid-point and gradient extremes, by giving species of rank 56 and 57 index value = 1, species of rank 55 and 58 value = 2, etc., until species 1 and 112 were given index values = 56. Index values ranged from 0 to 1.

ANOVA with Tukey's multiple comparison test (e.g. Sokal & Rohlf 1995) was used to test if the four species categories differed with respect to species properties. The gradient specific species properties were tested separately for each gradient. Pearson's product moment correlation coefficient was used to assess relationships between continuous predictor variables.

Logistic regression was performed for each of the three response variables by a two step procedure. First, the responses to each of the seven predictor variables were modelled separately. Next, we built logistic models for each response variable by including predictor variables and their interactions in order of decreasing *F* (and *p*) values. Checks were made at each stage that terms already in the model remained significant when new terms were added. Among models with the lowest number of degrees of freedom for included terms, and to which no more terms could be added that were significant at the $p < 0.05$ level, the model with lowest residual deviance was considered as best from a statistical point of view. A four-fold cross validation test (Venables & Ripley 2002) was conducted to assess the ability of competing models to predict the observations. We divided the observations into four subsets *i* ($i = 1, \dots, 4$) by the **speat** variable. Four reduced data sets $j = 1, \dots, 4$, corresponding to subsets *i* were made by leaving out subset *i* from the data. Each model was fitted to each reduced data set *j* in turn, and the model for set *j* used to calculate prediction errors (predicted residual deviance) for the corresponding subset *i*. Prediction errors were summed over $i = 1, \dots, 4$. The statistically best model always had the lowest prediction error among the competing models. Regression coefficients for significant terms in the statistically best models are reported as treatment contrasts.

Results

Gradient properties

The highest compositional turnover was observed for ecoclines (DCA axes 1 and 2), the lowest for environmental gradients (tree influence and slope; Table 1). Compositional turnover was always higher for ecoclines than for the environmental gradients correlated with them. Species density increased, mostly linearly, along DCA 1 and environmental gradients strongly correlated with DCA 1 (water and soil pH and total N in humus); weakly or unrelated to DCA 2 and environmental gradients correlated with it (tree influence and depth to water table) and moderately, mostly linearly, increasing along DCA 4 and the correlated gradient slope (Table 1).

Species properties

Sphagnum species differed from other species categories by being more frequent and occurring in plots with lower species density (Table 2). Gradient specific species properties **sptol** and **sptol** did not differ significantly among species categories for any gradient. Correlations greater than 0.3 between species properties were only found between **sptol** and **spfr** ($r = 0.5841, p < 0.0001, n = 1008$). **Sptol** was also correlated with **grlen** ($r = -0.3332, p < 0.0001, n = 1008$).

Species response curves

A unimodal or monotonous (determinate) model (**mod** = 1) was fitted to 820 (81.3%) of the 1008 species-gradient combinations (Table 3). The probability for fitting a determinate model did not differ significantly among species categories (Tables 3, 4), was unrelated to species richness, but significantly related to all other factors, as tested by logistic regression (Table 4). The probability for fitting a determinate model increased with species optima closer to gradient extremes, with increasing species frequency and with increasing gradient length, was higher for ecoclines than for environmental gradients, and decreased with increasing species tolerance. These five predictors all made independent significant contributions to prediction of **mod** (Table 5). Two interaction terms were included in the accepted model, both with negative values for the regression coefficient (Table 5); between **sptol** and **spfr** (indicating that the effect of wide tolerance was larger for less frequent species) and between **sptol** and **grlen** (indicating that the effect of an optimum near a gradient extreme was larger for gradients with low compositional turnover).

A unimodal model (**umod** = 1) was fitted to 450 (54.9%) of the 820 species-gradient combinations for which **mod** = 1 (Table 3). As with the probability for fitting a determinate model, the probability for fitting a unimodal model did not differ significantly among

Table 1. Patterns of variation in species richness along nine gradients modelled by fitting a polynomial regression model (of order ≤ 2) to total species number in plots, using plot position along gradient as predictor variable. Gradient properties **grtyp** (1 – DCA axis; 2 – environmental gradient) and **grlen** (gradient length in S.D. units) are also tabulated. Significance and sign of regression coefficients are indicated as follows: +++ : $p < 0.0001$; ++: $p < 0.001$; +, -: $p < 0.01$; (+), (-): $p < 0.05$; n.s.: $p > 0.05$.

Gradient	Gradient type (grtyp)	Gradient length (grlen)	Species richness pattern		
			Mean species richness	Significance of terms	χ^2
DCA 1	1	4.63	15-36	+++	–
DCA 2	1	3.64	18-27	n.s.	–
DCA 4	1	2.34	11-28	++	(–)
Slope	2	1.61	20-31	+	n.s.
TreeInf	2	1.57	24-28	n.s.	n.s.
WatTab	2	3.30	21-33	–	n.s.
pHWat	2	2.37	18-29	+++	(–)
pHSoil	2	2.99	17-39	+++	n.s.
N	2	3.33	17-38	+++	n.s.

species categories (Tables 3, 4), was unrelated to species richness and was significantly related to all other factors (Table 4). All except **spfr** were less strong predictors of **umod** than of **mod**. The probability for fitting a unimodal model decreased with species optima closer to gradient extremes and with increasing species frequency and tolerance, increased with increasing gradient length, and was higher for ecoclines than for environmental gradients. Only the two gradient specific species predictors **sptol** and **spopt** and their interaction made independent significant contributions to prediction of **umod** (Table 5). The probability for fitting a unimodal model thus decreased when species optima approached gradient extremes and with increasing species tolerance; although with lower effect of wide tolerance for species with optima close to gradient extremes.

A skewed unimodal model (**sumod** = 1) was fitted to 148 (32.9%) of the 450 species-gradient combinations for which **sumod** = 1 (Table 3). The probability for fitting a skewed unimodal model was significantly (although not strongly) related to three predictors only; increased with species optima closer to gradient extremes and decreased with gradient length and species frequency. The only predictor retained in the full model was **spopt** (Table 5).

Discussion

Factors determining the shape of species response curves along gradients

The shape of species response curves is, to a considerable extent, determined by species and gradient properties. This is most clearly the case for determinate (unimodal or monotonous) vs. indeterminate responses: a determinate model is most likely to be found for a frequently occurring species that occupies a narrow portion of a long gradient, occurring near one gradient extreme. This is in accordance with expectations; all factors found to increase the probability of a determinate response contribute to systematic variation in species abundance along a gradient.

Our result that only the gradient specific species properties contribute independently to predictability of unimodal vs. monotonous responses does not, as might first seem to be the case, contradict what is generally accepted as a truth; that the proportion of species with unimodal response increases with increasing α -diversity (in the meaning species turnover; Vellend 2001) along a gradient. We also found a significant relation-

Table 2. Differences in species characteristics (overall and as classified to four species groups) with respect to the species explanatory variables **spfr**, **sprich**, **sptol** and **spopt** – position of optima relative to gradient mid-point (0) and gradient extreme (1). Variables **sptol** and **spopt** are reported for the DCA 1 gradient. Differences among groups are tested by standard ANOVA, with the variable in question as response variable and species category as factor (F statistic and p values are given). Among category comparisons are performed using Tukey's method. Means sharing at least one letter are not significantly different at the $p < 0.05$ level.

Species category (spcat)		Species frequency (spfr)	Species richness (sprich)	Species tolerance (sptol)	Position of species optimum(spopt)
Vascular plants ($n = 49$)		0.224ab	30.50b	0.616a	0.531a
Mosses ($n = 36$)		0.190a	33.32b	0.585a	0.502a
<i>Sphagnum</i> ($n = 9$)		0.363b	23.27a	0.640a	0.669a
Hepatics ($n = 18$)		0.176a	33.87b	0.655a	0.377a
All species ($n = 112$)		0.217	31.37	0.614	0.509
ANOVA for difference	$F_{3,108}$	3.55	11.54	0.49	2.26
among species groups	p	0.0169	< 0.0001	0.6882	0.0859

Table 3. Species response modelling results, as summarized by the **mod**, **umod**, **sumod** response variables for the total species composition and for each species category. No pair of species categories differs significantly ($p < 0.05$) with respect to any of the response variables [logistic regression within species category (vascular plant (1), moss (2), *Sphagnum*(3) or hepatic (4)) as factor, analysed within a generalized linear framework (logit link function and binomial error distribution, with F test); among-category comparisons by Tukey's method].

Species category	Estimated mean for response variables		
	Probability of (linear or unimodal) model (vs indeterminate model) (mod = 1)	Probability of unimodal (vs monotonous) model (umod = 1)	Probability of skewed (vs symmetric) unimodal (sumod = 1)
Vascular plants	0.828	0.564	0.296
Mosses	0.809	0.550	0.382
<i>Sphagnum</i>	0.840	0.500	0.294
Hepatics	0.772	0.528	0.333
Total	0.813	0.549	0.329

ship between gradient length (as tested singly) and unimodal vs. monotonous response in our study, and the **sptol** and **grlen** variables are strongly correlated. The effect of gradient length thus contributes to the effect of relative species tolerance in the full model of probability for unimodal vs. monotonous responses. The stronger predictive power of relative species tolerance than that

of gradient length shows that the proportion of species with unimodal response varies among gradients that differ in compositional turnover (see Bongers et al. 1999) because compositional turnover influences the relative abundance of species response curve shapes by controlling the distribution of relative species tolerances (the fraction of the gradient occupied by each species)

Table 4. The influence of single predictor variables; **grtyp** = gradient type (DCA axis (1) or environmental gradient (2)); **grlen** = gradient length (in S.D. units); **spcat** = species category (vascular plant (1), moss (2), *Sphagnum* (3) or hepatic (4)); **spfr** = species frequency; **sprich** = species richness (mean number of species in plots, using subplot frequency of the focal species as weights); **sptol** = species tolerance; fraction of gradient along which the focal species occurs; and **spopt** = position of species optimum on a scale from gradient mid-point (0) to gradient extreme (1) on each of the three response variables; **mod**; probability of (linear or unimodal; **mod** = 1) vs indeterminate model (**mod** = 0), **umod**; for **mod** = 1, probability of unimodal (**umod** = 1) vs monotonous (**umod** = 0) model, and **sumod**; for **umod** = 1, probability of skewed (**sumod** = 1) vs symmetric (**sumod** = 0) model, as modelled by logistic regression within a generalized linear framework (logit link function and binomial error distribution). Predictor +1 refers to the null model. df = model degrees of freedom. F and p refer to a F test of the model by which the difference in deviance between the null model ($y \sim +1$) and the model is compared with the deviance of the model, taking the degrees of freedom into account. The Sign column gives the sign of regression coefficients significant at the $p < 0.05$ level.

Response variable	Predictor	df	Deviance	F	p	Sign
mod	+1	1007	969.94			
	factor(grtyp)	1	53.08	53.32	< 0.0001	–
	grlen	1	74.77	76.73	< 0.0001	+
	factor(spcat)	3	2.80	0.94	0.4217	
	spfr	1	11.12	11.25	0.0008	+
	sprich	1	0.28	0.28	0.5940	
	sptol	1	156.09	148.75	< 0.0001	–
	spopt	1	137.09	157.23	< 0.0001	+
umod	+1	819	1128.94			
	factor(grtyp)	1	9.46	9.45	0.0022	–
	grlen	1	19.78	19.76	< 0.0001	+
	factor(spcat)	3	1.23	0.41	0.7477	
	spfr	1	34.02	34.04	< 0.0001	–
	sprich	1	3.62	3.61	0.0577	
	sptol	1	89.45	89.07	< 0.0001	–
	spopt	1	72.02	71.64	< 0.0001	–
sumod	+1	449	570.05			
	factor(grtyp)	1	0.83	0.82	0.3649	
	grlen	1	7.86	7.82	0.0054	–
	factor(spcat)	3	3.01	0.99	0.3955	
	spfr	1	5.53	5.52	0.0193	–
	sprich	1	0.23	0.23	0.6326	
	sptol	1	0.00	0.00	0.9874	
	spopt	1	15.75	15.70	0.0001	+

Table 5. Statistical summaries of logistic regression models (as found within a generalized linear framework, i.e. with logit link function and binomial error distribution) for the influence of predictor variables; **grtyp** = gradient type (DCA axis (1) or environmental variable (2)); **grlen** = gradient length (in S.D. units); **spcat** = species category; vascular plant (1), moss (2), *Sphagnum*(3) or hepatic (4); **spfr** = species frequency; **sprrich** = species richness (average number of species in plots, using subplot frequency of the focal species as weights); **sptol** = species tolerance; fraction of gradient along which the focal species occurs; and **spopt** = position of species optimum on a scale from gradient mid-point (0) to gradient extreme (1) on each of the three response variables; **mod**; probability of (linear or unimodal; **mod** = 1) vs indeterminate model (**mod** = 0), **umod**; for **mod** = 1, probability of unimodal (**umod** = 1) vs monotonous (**umod** = 0) model, and **sumod**; for **umod** = 1, probability of skewed (**sumod** = 1) vs symmetric (**sumod** = 0) model. *F* and *p* refer to *F* tests of the change in deviance between nested models. *df* = model degrees of freedom. Regression coefficients for significant terms are given as treatment contrasts.

Response variable	Predictor	df	Deviance	<i>F</i>	<i>P</i> (<i>F</i>)	Coefficients
mod	null	1007	969.94			0.207
	sptol	1	156.09	78.34	<0.0001	-0.521
	spopt	1	115.67	58.05	<0.0001	9.926
	grlen	1	37.63	18.88	<0.0001	1.069
	spfr	1	23.46	11.77	0.0006	0.249
	sptol:spfr	1	16.99	8.53	0.0036	-0.228
	spopt:grlen	1	15.96	8.01	0.0048	-2.028
	factor(grtyp)	1	8.85	4.44	0.0353	-0.419
umod	null	819	1128.94			7.188
	sptol	1	89.45	88.24	<0.0001	-7.696
	spopt	1	92.17	90.92	<0.0001	-0.546
	sptol:spopt	1	11.07	10.92	0.0010	5.395
sumod	null	449	570.05			-1.449
	spopt	1	15.75	15.66	0.0001	1.467

and the distribution of species' points of gravity along the gradient. The mean relative tolerance decreases with increasing compositional turnover along a gradient, and raises the probability for species response curves of being unimodal. Furthermore, the higher the compositional turnover, the larger fraction of the species will be situated sufficiently far away from gradient extremes to avoid truncation of response curves (which raises the probability for response curves to be monotonous). We expect the power of gradient length as predictor of unimodal vs. monotonous response curves will increase with increasing variation in compositional turnover along gradients. We thus agree with Oksanen & Tonteri (1995) that information on compositional turnover is essential in all studies of species response curve shapes.

Unimodal and monotonous models were almost equally frequently distributed over the six environmental gradients we studied, with species turnovers in the range 1.5 - 3.4 S.D. units. Compared to monotonous and indeterminate models, less than half of the fitted response curves were unimodal. Ordination studies performed in a variety of ecosystems show that amounts of compositional turnover in this range is typical, even of major environmental complex gradients (R. Økland 1990). This result therefore questions the general applicability of the unimodal response curve (Austin 1976, 1987; Minchin 1989) for the 'real' gradients faced by the ecologist in their study area. Our results suggest that a mixture of unimodal and monotonous responses is typical of 'real' gradients; species with optima near the gradient mid-point mainly having unimodal and species

with optima near gradient ends mainly having monotonous responses. Our result, that the relative abundance of unimodal curves increases with increasing gradient length, is in accordance with the view that all species have unimodal responses to abstract gradients (of infinite length) that extend in both directions beyond the limits of all species (Austin 1990).

Our results show that, among species with an unimodal response, skew vs. symmetry is predictable from species or gradient properties only to a minor extent. The only independently significant predictor in the full model is the position of species optima. Dependence of skewness on the relative position of species optima is, however, expected, because the extent to which unimodal response curves are truncated increases with closeness of species optima to the gradient end-point. The decreasing probability for response curves to be skewed with respect to longer gradients, as apparent from separate tests (Table 4), partly arises because, with short gradients, both sides of most response curves are truncated, partly because the fraction of species that avoid truncation of response curves increase rapidly with increasing gradient length for long gradients. For low turnover gradients (slope and tree influence) we find probabilities for unimodal responses to be skewed that are higher than 0.5, while for the other, higher turnover, gradients we invariably find fewer skewed than symmetric unimodal models (e.g. for DCA 1, only 21% of unimodal response curves are skewed). The proportion of skewed unimodal response curves is generally lower in our study than in most other studies

(Austin et al. 1984, 1994; Austin 1987; Austin & Meyers 1996), while it is in accordance with the slightly higher abundance of symmetric than of skewed responses demonstrated by Minchin (1989). Our results suggest that this variation, within and among studies, in the relative importance of skewed and symmetric unimodal responses, is due to variation in gradient properties, notably gradient length. We find no difference between gradient types in this respect, but cannot rule out the possibility of an effect in the way environmental gradients are scaled from a single study (R. Økland 1986b, 1992; Minchin 1989).

In contrast to previous studies (e.g. Minchin 1989), we find no significant differences among species categories with respect to response curve properties. Instead, our study highlights gradient length and gradient specific species properties such as tolerance and the position of the optimum, as major determinants of response curve shape. These results may indicate existence of general rules for species response curve shapes along gradients that are valid for plants regardless of structural, life strategy or taxonomic group. More studies are, however, needed to assess the general applicability of these findings (cf. Austin & Gaywood 1994; Austin et al. 1994; Austin 1999b) and to decide if species response curve shapes make an exception to the accepted notion that dividing species into functional types (Semenova & van der Maarel 2000) is important when their ecological performance is to be understood (Peet 1978; Minchin 1989; Diaz et al. 1999).

Effect of re-arrangement of plots and rescaling of gradients by DCA ordination on response curve shape and its relevance to the nature of complex environmental gradients

The significant differences in probability of different response curve shapes (determinate vs. indeterminate, unimodal vs. monotonous, but not skewed vs. symmetric unimodal) observed between DCA ordination axes and the environmental gradients most strongly correlated with these axes can be almost entirely accounted for by the higher compositional turnover of the former. In our opinion, this reflects a real difference between complex gradients compared with single environmental gradients that arises because species do not respond to single environmental gradients, but to a complex of factors that vary more or less in relation to each other. The complex gradient and its substitute, the ordination axis, capture more detail in the responses of a larger fraction of the species, resulting in larger compositional turnover along the complex gradient. Furthermore, DCA ordination re-orders plots to a sequence that accords much better with the underlying,

complex, factor governing the distribution of a large fraction of the species than each of the measured, noisy environmental variables (ter Braak 1987; McCune 1997). Species abundance patterns are therefore more predictable from DCA ordination scores than directly from measured environmental variables (Ejrnæs 2000). This is reflected in higher compositional turnover along DCA axes than along single environmental gradients. We hypothesize that higher predictability of response curve shapes in general, and a relatively higher fraction of unimodal response curves in particular, are typical characteristics of complex gradients compared to the single environmental gradients they consist of. This is at odds with Minchin's (1989) interpretation of the apparent increase in the share of unimodal response curves along DCA axes (compared to single environmental gradients) as an artefact of the ordination method.

We find no support for Minchin's (1989) suggestion that DCA tends to rescale gradients in order to maximize the number of *apparently symmetric* responses (also see R. Økland 1986b). The extent to which DCA increases the fraction of symmetric response curves may be data dependent or may be a result of the higher compositional turnover of complex gradients than of single environmental gradients. The non-linear rescaling process in DCA will bring about a change of the fraction of symmetric response curves if response curves are skewed with respect to an environmental gradient due to systematic variation in rate of compositional turnover along the gradient (as originally scaled). The hypothesis that species response curves are generally skewed with tails in the direction of the optimal habitat along the gradient (Austin 1990; Austin & Gaywood 1994) will thus not be a property of this gradient and the species, but of the original scaling of the gradient. For instance, this can be shown for the eucalypt tree species data used to provide empirical support for this hypothesis (Austin et al. 1994): sets of similarly skewed response curves are turned less skewed by nonlinear DCCA rescaling (R. Økland unpubl.) because the skew is brought about by the gradual reduction in compositional turnover per unit of the original scaling towards gradient end-points. Furthermore, we find no relationship between species richness trends along gradients and the symmetry of response curves in our data.

It has been argued that there are no such things as a 'correct' or 'best' scaling of gradients, and that all scalings of gradients are essentially arbitrary (Wartenberg et al. 1987; Peet et al. 1988; Minchin 1989). Nevertheless, we argue (also see Wilson & Mohler 1983; R. Økland 1986a, 1992; Peet et al. 1988) that scalings in units of compositional turnover are *biologically more meaningful* than other scalings because they express the biological response of a majority of the species along

the underlying gradient. Our results indicate that rescaling in terms of compositional turnover does not necessarily make response curves more symmetrical than expected from the increased gradient length. Anyway, the scaling used for a gradient influences response curve properties so strongly that any discussion of curve shape without reference to scaling is meaningless.

Implications for ordination methodology

Implicit in ordination methods are assumptions about species response curves that are often untested (Austin & Gaywood 1994). All currently available ordination methods do, however, assume that all species have the same response curve. This assumption will never be satisfied with real data. Our study, as well as a large number of studies of comparable data sets (Austin 1976, 1980; Austin et al. 1984, 1994; Austin & Smith 1989; Austin & Gaywood 1994), show that all data sets, except perhaps the most homogeneous, in which all variation in species abundances is pure noise, will exhibit a mixture of species response curves; unimodal, monotonous and apparently random (indeterminate). Furthermore, even with long gradients a considerable fraction of the species will have truncated realized response curves because their optima fall outside the sampled portion of the gradient (ter Braak & Looman 1986).

The variation in response curve shapes is an inevitable cause of distortions in ordinations (R. Økland 1990), that cannot be amended within the concept of ordinations based upon one statistical model.

The strong focus in the vegetation ecological literature on species with skewed unimodal response curves (Austin 1980; R. Økland 1986b; Minchin 1989; Austin & Gaywood 1994; Austin et al. 1994; Bongers et al. 1999) does not agree with the low number of such species in our data, compared with species that are lacking any systematic relation to the gradient(s) and species with monotonous response curves. Mathematically, skewness represents a far less serious deviation from symmetric unimodality than a monotonous (or indeterminate) response. A moderate fraction of species with skewed response curves is therefore probably of less importance for the performance of ordination methods.

Conclusions and suggestions for further studies

More empirical evidence is needed before we can generalize about frequency distributions of response curve shapes along 'real' gradients, to the extent that these generalizations form a coherent vegetation theory (Austin & Smith 1989; van der Maarel 1989; Austin

1999b; Oksanen & Minchin 2002). However, our results point to one factor of primary importance for the frequency distribution of species response curves: the compositional turnover along the underlying gradient: unimodal curves increase, monotonous and indeterminate responses decrease with increasing turnover. Furthermore, we demonstrate systematic variation among species that replace each other along a gradient in response curve shape that is to a large extent predictable from the positions of species' points of gravity along the gradient. These results give promises for an improved theoretical foundation, e.g. for testing of ordination methods, that may replace the 'robustness criterion' of Minchin (1987) by which the best method is considered to be the one that has the best gradient recovery over a range of community pattern types (see criticism by R. Økland 1990).

Our focus is on general properties of species response curves, as determined by the standard HOF modelling procedure by which response models were selected by a strict use of a fixed significance level of $p = 0.05$. Further insights into the nature of species response curves and the factors shaping them may be obtained by consideration not only of the type, but also of the distinctness of fitted response models, as indicated by the degree of superiority over alternative models, and the variation in species abundances and occurrences they account for. We find systematic variation along gradients in the frequency of occurrence of unimodal and monotonous response curves. Such variation will confound tests of the propositions of Gauch & Whittaker (1972) concerning distributions of optima of major and minor species along gradients. Valid tests of these propositions will, however, be possible on data for gradients with high compositional turnover (that comprise segments along which response curves for almost all species are expected to be unimodal). In these, and most other tests, due consideration of the effect of scaling is needed.

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